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The deep-sea macrobenthos on the continental slope of the northwestern Mediterranean Sea: a quantitative approach

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Abstract

As part of the ECOMARGE operation (J.G.O.F.S. France), macrobenthic assemblages in the Toulon Canyon were described and quantified on the basis of sampling carried out between 250 and 2000 m depth on the Mediterranean continental slope. Results show that Mediterranean bathyal assemblages are made up mainly of continental shelf eurybathic species. The qualitative and quantitative composition of populations varies with depth on the slope and also varies with station position at equivalent depth, whether on the flanks or in the canyon channel. Various analyses have provided evidence on the factors responsible for this population distribution pattern. No single factor emerges as predominant, but rather a group of factors, which are related to the nature and origin of sediments and more particularly their grain size distribution, geochemical composition and mode of transportation and sedimentation (benthic nepheloid or originating from the water column), act in conjunction to determine the pattern. Comparison with ocean continental slopes shows that in the Mediterranean Sea the absence of tidal current modifies the trophic structure of the macrobenthic assemblages, which are characterized by a dominance of surface and subsurface deposit feeders as compared to a dominance of suspension feeders and carnivores in the upper and median part of the slope in the ocean. Surface dumping of dredge spoil at the canyon head and channelling of waste induces an

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increase of organic matter and pollutant concentrations in sediment from the upper part of the canyon channel but does not give rise to any marked population degradation.

1. Introduction

The continental slope and more particularly the canyons cutting across it have long been recognized as zones of matter and energy transfer between the continental shelf and the deep ocean (Griggs et al., 1969; Gardner, 1989). Since 1983, the ECOMARGE operation, which is part of the program Joint Global Ocean Flux Study France, has involved a series of multidisciplinary investigations to study the functioning of continental margin ecosystems (Monaco et al., 1990). Research carried out on the continental slope has focused mainly on the qualification and the quantification of advective and convective particle fluxes and their variation with time, and on the impact of matter and energy transfer to the water-sediment interface. It is in an attempt to shed light on the latter question that studies have been carried out on the macrobenthic assemblages of a Mediterranean canyon, the Toulon Canyon.

Transfers of matter and energy from the continental shelf and the water column to the continental slope have a strong impact on the distribution and composition of benthic assemblages, which constitute the biological testimony of the environmental conditions. From the quantitative and qualitative points of view, deep macrobenthic assemblages have been studied in many regions of the world's oceans, notably those of the continental slope (Sanders et al., 1965; Griggs et al., 1969; Grassle et al., 1979; Rowe and Headrich, 1979; Pearce et al., 1979; Rowe et al., 1982; Blake and Doyle, 1983; Pfannuche et al., 1983; Romero-Wetzel and Gerlach, 1991; Blake and Grassle, 1994; Blake and Hilbig, 1994), but the lack of quantitative data on the deep Mediterranean benthos has been pointed out by several authors (Peres, 1982; Fredj and Laubier, 1985; Bouchet and Taviani, 1992; Laubier and Emig, 1993). Our present knowledge is limited to qualitative and descriptive aspects of the deep sea fauna. How the deep Mediterranean ecosystem functions, compared with other ecosystems of the world's oceans, is largely unknown (Fredj and Laubier, 1985). Macrobenthic assemblages at the limit of the continental shelf and the upper part of the slope have been described mainly on the basis of dredgings rarely exceeding 1000 m depth in the northwestern region of the Mediterranean Sea by Picard (1965), Carpine (1970), Reyss (1970), Bourcier (1969), Falconetti (1980), and in the northeastern region by Vamvakas (1970) and Chardy et al. (1973). The rare quantitative data obtained by sediment cores have been reported by Tchukhchin (1964), Cattaneo and Albertelli (1983), Tahey et al. (1992), Tselepides and Eleftheriou (1992), Bourcier et al. (1993) and Gerino et al. (1994).

In view of this gap in our knowledge of the Mediterranean Sea, the primary aim of this study in the Toulon Canyon was to qualify and quantify the macrobenthic assemblages of the continental slope, to determine the factors responsible for the distribution and composition of these assemblages, to analyze the impact of the channelled

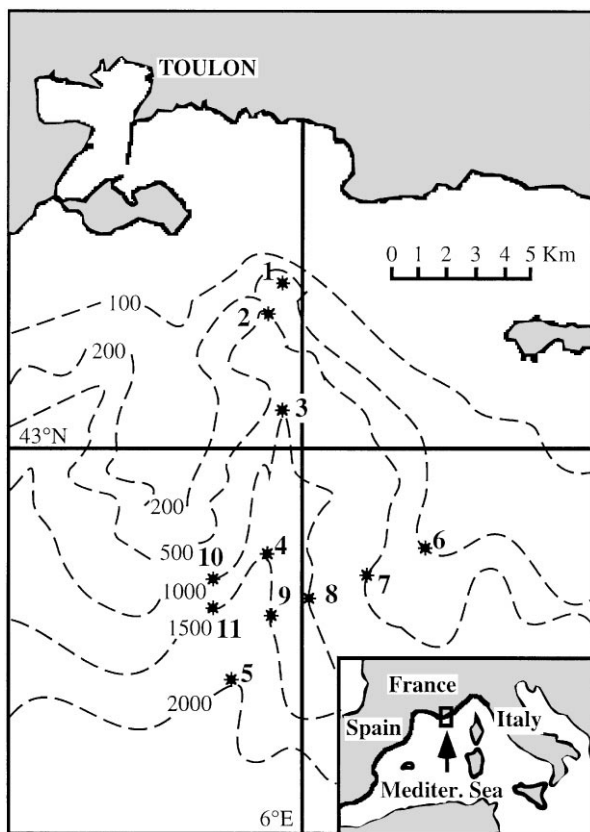


Fig. 1. Locations of the stations in the Toulon Canyon.

inputs in the canyon axis and to compare the results obtained with those from the Atlantic margin.

In the northwestern Mediterranean Sea, the coast of Provence (from Marseilles to the Italian border), where the Toulon Canyon is located (Fig. 1), is characterized by a narrow continental margin that extends between 20 and 30 km offshore. Off Toulon, the continental shelf represents one-half or one-third of the continental slope and presents an average slope of the order of 2–3%. The Toulon Canyon (Poydenot, 1993) is a linear valley lying north–south, perpendicular to the base of the slope. It is 18 km long and 9 km wide, with a height differential of 2100 m. The canyon is not an extension of an existing river on the continent. The canyon walls are asymmetrical. The west flank represents 43% of the canyon’s surface and is strongly sloping (26.7%). The east flank is more eroded, represents 57% of the canyon’s surface and slopes more gently (21.1%). The width of the channel increases from about 200 m at the canyon head to more than 1000 m at the deep fan outlet.

Water circulation in the canyon follows a complex pattern. It is influenced by the general flow of the Liguro-Provençal current flowing from east to west (Millot, 1990), and by meteorological conditions inducing upwelling currents in the canyon channel with north–northwesterly winds, or downwelling currents with east, south and south-westerly winds (Bourcier, 1969; Millot and Wald, 1980; Poydenot, 1993). In the absence of a large coastal river, material contributions to the continental slope mainly originate from the continental shelf in the Toulon area and from the Liguro-Provençal current (Poydenot, 1993). Surface dumping of dredge spoil from Toulon harbour at the canyon head is added to these inputs on the sea floor between 250 and 500 m depth. The frequency of these deposits, in tonnages that are confidential (military zone), varies from once every six months to once per year.

2. Materials and methods

2.1. Sampling

Eleven stations were studied in Toulon Canyon, distributed along three transects (canyon channel, east flank, west flank) between 200 and 2000 m depth (Fig. 1). Because of the presence of rocky cliffs on the west flank, only two stations, located at 1000 and 1500 m depth, could be sampled. Most of the samples were taken between May and July 1988. At each station, with coordinates specified in Table 1 (Toran navigation system), samples were randomly collected within a circle not exceeding 1/10 mile from the reference point. The box core used is the FLUCHA corer, which retrieves relatively undisturbed sediment samples with a surface area of 6.25 dm² (2.5 × 2.5 dm) and a height of 30–40 cm. Six replicate cores were taken at each station. In these cores, only the upper 12 cm of the sediment was collected, corresponding to a sediment volume of 7.5 dm³ per core. A total of 66 samples were sieved through

Table 1
Depths, sampling dates and station coordinates

Stations	Depths (m)	Dates	Latitude N	Longitude E
CTL 1	250	15/1/88	43°03'50	05°58'90
CTL 6	250	4/7/88	42°57'80	06°03'50
CTL 2	500	5/5/88	43°02'72	05°59'25
CTL 7	500	29/6–4/7/88	42°57'10	06°01'75
CTL 8	1000	29/6/88	42°56'80	06°00'50
CTL 10	1000	8/7/88	42°57'30	05°57'30
CTL 3	1100	15–24/1/88	43°00'71	05°59'71
CTL 4	1500	7/5/88	42°57'70	05°59'20
CTL 9	1500	28/6/88	42°56'40	05°59'40
CTL 11	1500	7/7/88	42°56'60	05°57'70
CTL 5	2000	5/5/88	42°55'17	05°58'52

a 500 μm mesh and then sorted. In most cases, organisms were identified to species level.

Since the surface layer is more representative of recent inputs to the canyon, chemical analysis of sediment at each station was carried out on an average sample obtained by the mixing and homogenization of part of the first cm of six replicate cores.

2.2. Geochemical analysis

Analyses were carried out on the sediment fraction smaller than 63 μm sifted by wet sieving. Loss of ignition (LOI) was obtained by heating in a furnace at 550°C. Organic carbon was measured by oxidation by the chromic acid method (FAO, 1975).

Determination of the total content of heavy metals (Cu, Pb, Cd, Zn, Cr, Ni, CO, Mn and Fe) was carried out after digestion of sediments by adding 1 g of sediment to 10 ml of the mixture HCL + HNO₃ (3 + 1 V/V) at 120°C for 2 h with a reflux condenser (Arnoux et al., 1981). Each metal assay was carried out by flame atomic absorption spectroscopy in air-acetylene flame for Cu, Pb, Cd, Zn, Ni, Co, Mn, in N₂O-acetylene flame for Cr and by spectrophotometry of the complex given with the o-phenantroline for Fe (Arnoux et al., 1981).

2.3. Biological analysis and data processing

Classical analytical and synthetic methods (Legendre and Legendre, 1984a, b) were used to assess the spatial dynamics of the assemblages. Interpretation of results is based on faunal data expressed as species richness, species density, dominance and biomass. After CaCO₃ elimination with HCl, the biomass was determined by drying the organisms at 60°C in an oven until the sample weight remained constant.

Rowe et al. (1982) worked in an environment similar to the Toulon Canyon (Hudson Canyon, western atlantic), and in order to facilitate comparison with their results, when possible we applied the same processing methods they used. Homogeneous groups of stations were singled out by cluster analysis (Legendre and Vaudor, 1991) applied to a similarity matrix obtained by the coefficients of Sorensen (Sorensen, 1948) and Whittaker (Whittaker and Fairbanks, 1958), which are, respectively, a qualitative coefficient based on the presence-absence of the species and a quantitative coefficient based on their dominance.

In order to give evidence of rare species effect on the clusterings we used a third similarity coefficient, the Normalized Expected Shared Species (NESS) (Grassle and Smith, 1976). NESS was used for analyses of stations with combined replicates, and the number of individuals (m) was set at 10 and 30.

The study of species association was carried out using, in R mode, the Dice index (Dice, 1945), whose formulation is identical to the Sorensen index (Legendre and Legendre, 1984). Species represented by a single individual at a station were eliminated from this procedure. The diversity measurements were carried out using two widely used methods (Gage and Tyler, 1991), the rarefaction curves (Sanders, 1978) modified by Hurlbert (1971) and the Shannon-Wiener information function (H')

(Shannon and Weaver, 1963) and its associated evenness value (J) (Pielou, 1966). Each H' and J station value was obtained by pooling data from the six replicate cores collected at a station. The Shannon Wiener index was calculated using the base log_e.

The relation between density or biomass and depth was investigated by means of generalized linear models (McCullagh and Nelder, 1989). In order to determine the main factors responsible for the composition and the structure of the assemblages, a factorial correspondence analysis (FCA) was carried out (Benzecri, 1973). The advantage of this method is that both the lines and columns of a contingency table can be represented on the same projection planes. Given the large number of collected species, of which few contribute strongly to the inertia of the first axes, species represented by a single individual at a station were eliminated. From the results obtained by the FCA, correlations (Coefficient of Spearman) were calculated between the ordination of variables on the adopted axes and the different chemical and physical parameters analysed in sediments of the surface layer (Vincent, 1981). Interpretation of results was based on the presence of biological indicators (Picard, 1965; Carpine, 1970; Peres and Picard, 1964; Peres 1982; Bourcier 1976). These indicators can be either specific to an original assemblage (characteristic species) or to one or several grain size fractions (silts, sands, gravels, etc.). In other cases, they can mark particular environmental conditions such as sediment instability or pollution, or they can have no particular ecological requirements (wide ecological range species). Finally, the assemblages were characterized by their nutrition mode using indications provided notably by Coull (1977), Fauchald and Jumars (1979), Jumars et al. (1990) and Gage and Tyler (1991).

According to Blake and Grassle (1994), organisms for which the identification was uncertain (e.g. juveniles, anterior fragments, etc.) were used only for density and biomass measurements and were not included in calculations of similarity, diversity indexes and multivariate analysis.

3. Results

3.1. Geochemical analysis

Table 2 presents percentages and concentrations of various elements analyzed in the surface layer of Toulon sediments. The geochemical characteristics of continental slope sediment resulting from the particle inputs, either transported along the bottom by the nepheloid benthic layer or originating from the water column, depends on several geological, oceanic and anthropogenic factors (Karl et al., 1983; McGrail and Carnes, 1983). With the exception of stations at the head of the canyon that are influenced by currents linked to the shelfbreak, fine fraction percentages are greater than 70% for all the canyon stations. The presence in canyon sediments of *Posidonia* fibers originating from the continental shelf (Poydenot, 1993) results in high percentages of loss of ignition in both channel and flank stations below 500 m depth. However, stations located in the channel of the Canyon are characterized by higher organic carbon percentages than the other stations, associated with strong concentrations of

Table 2
Granulometric and geochemical characteristics of the superficial Toulon canyon sediments

Stations depth	(m)	Channel						East flank					West flank		
		CTL 1	CTL 2	CTL 3	CTL 4	CTL 5	CTL 6	CTL 7	CTL 8	CTL 9	CTL 10	CTL 11			
		250	500	1100	1500	2000	250	500	1000	1500	1000	1570			
Fraction < 63 µm	%	35.76	71.12	80.32	88.4	83.24	36.9	77.19	93.57	92.88	95.24	94.12			
L.O.I. (550°C)	%	7.90	14.7	13.41	12.16	11.78	5.8	13.32	14.41	13.37	14.22	14.1			
Organic C	%	2.20	3.48	3.10	1.44	0.78	1.00	1.11	1.24	0.94	1.00	0.93			
Copper	µg g ⁻¹	32.74	57.7	35.00	32.1	46.5	8.44	21.0	27.1	26.3	24.6	26.8			
Lead	µg g ⁻¹	71.2	58.9	50.3	70.0	21.5	15.1	51.8	30.7	23.5	31.0	28.7			
Cadmium	µg g ⁻¹	1.15	1.36	1.48	1.81	1.49	1.29	1.48	1.82	1.83	1.84	1.74			
Zinc	µg g ⁻¹	163	202	120	134	80	83.8	107	94.1	86.3	108	81.2			
Chrome	µg g ⁻¹	17.1	39.5	38.0	48.0	40.5	27.5	41.8	53.5	50.6	49.5	51.1			
Nickel	µg g ⁻¹	13.75	28.8	29.2	43.8	38.5	20.1	37.0	46.2	46.1	46.5	46.9			
Cobalt	µg g ⁻¹	4.58	6.89	6.53	9.52	8.55	6.68	7.7	10.4	10.6	10.1	11.0			
Manganese	µg g ⁻¹	176	218	227	899	739	204	341	876	1174	708	1680			

lead, zinc and copper, notably between 250 and 1100 m depth. These high-concentrations mark the preferential deposition area of the dredge spoils originating from Toulon roadstead, which are rich in organic elements and heavy metals (Romana et al., 1991) dumped between stations CTL1 and CTL2. With the exception of lead and zinc, the other heavy metal concentrations, notably at the canyon flanks, increase with increasing depth as a result of natural sedimentation of fine particles with high metal content (Förstner and Wittmann, 1979) transported by the general or local circulation. Manganese, and to a lesser degree nickel and chromium are more particularly carried by the Liguro-Provençal current (Arnoux et al., 1992).

3.2. *Biological analysis*

3.2.1. *Species accumulation*

We first verified whether the sampling carried out at each station collected the majority of species present. Species accumulation curves were constructed by plotting the addition of new species as a variable dependent on an increasing number of cores for each station. The species accumulation curves in our assemblages (Fig. 2) indicate that, except for stations located at 250 m depth (CTL1, CTL6), where we could have benefitted from more samples, the area sampled at the other stations was more than enough for capturing the majority of the species present and for estimating various parameters of the benthic assemblage structure. In fact, it appears (Fig. 2) that three samples would have been sufficient to assess variation.

3.2.2. *Species richness and density*

There is a strong decrease in the species richness with depth, ranging in the canyon channel from 124 species at station CTL1 (250 m) to 31 species at station CTL5 (2000 m) (Table 3). The decrease in species is in fact particularly marked between 250 and 1000 m depth. Below 1000 m, a certain stabilization of the species number is apparent.

The variations in fauna density (numbers m^{-2}) for individual samples as a function of depth (X) were described as usual (Rowe et al., 1982; Gage and Tyler, 1991) by a log-linear equation: $\log_{10}(\text{density}) = a + b(X)$ (1) and are shown in Fig. 3.

Firstly, to compare the mean densities at the different stations, the equality of variances was verified. However, since the homoscedasticity hypothesis cannot be held, we used generalized linear models (Glim 4, 1993; McCullagh and Nelder, 1989), with density at each station weighted by the inverse of the corresponding standard deviation. In this way, we estimated the parameters of the regression equation (1) by the maximum likelihood method. The statistical significance of parameters was assessed by considering the increase of the log-likelihood statistic between two hypotheses (with and without this parameter) (McCullagh and Nelder, 1989). The difference is distributed as a chi square in the absence of the effect of the considered variable.

The estimated regression equation is

$$\text{Log}_{10}(\text{density}) = 6.9 - 0.0011X$$

(Depth effect: $\text{Chi}^2 = 48.30$, 1 df, $p < 0.001$).

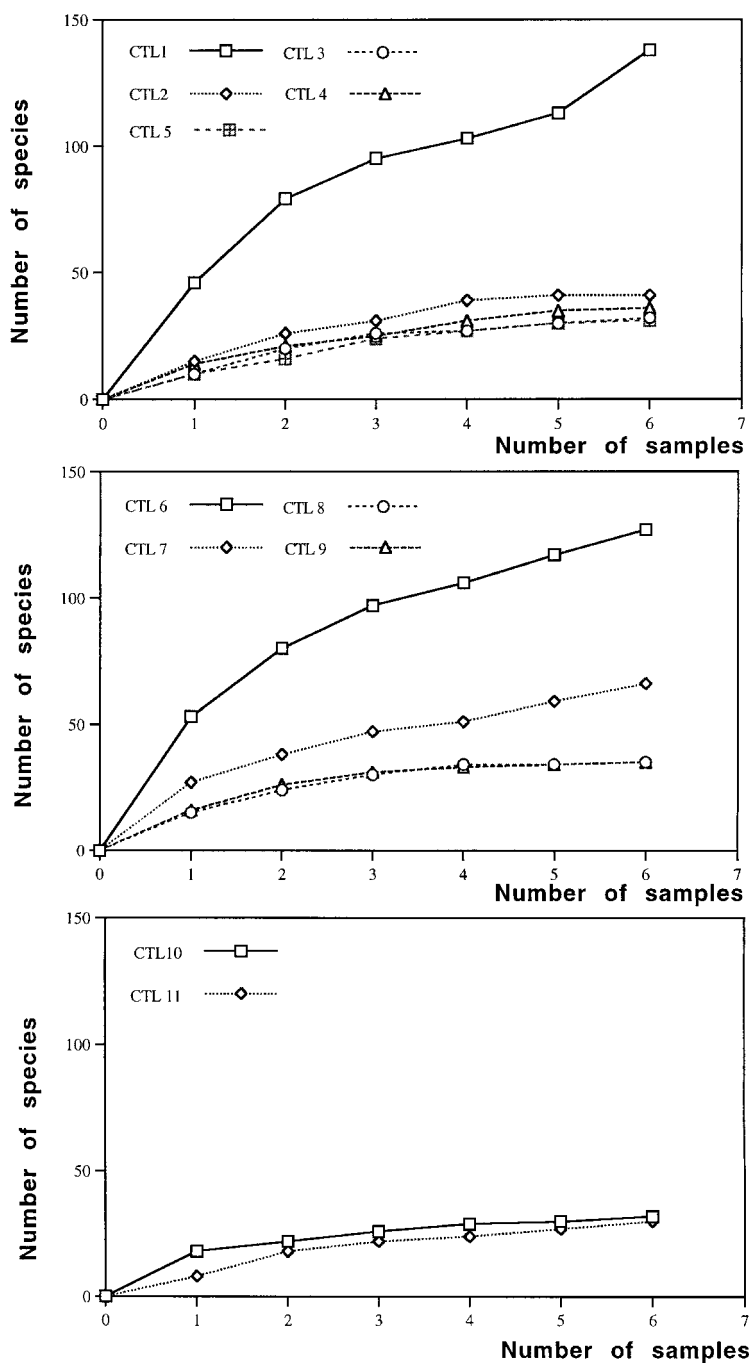


Fig. 2. Species recruitment curves.

Table 3
Infauna – assemblage parameters in the Toulon canyon stations

	Channel						East flank				West flank	
	CTL 1	CTL 2	CTL 3	CTL 4	CTL 5	CTL 6	CTL 7	CTL 8	CTL 9	CTL 10	CTL 11	
Depth (m)	250	500	1100	1500	2000	250	500	1000	1500	1000	1570	
No. species	98	36	25	23	21	93	51	21	22	26	24	
X specimens m ⁻²	1000	176	149.3	306.7	210.7	1272	552	202.7	181.3	397.3	237.3	
(± CL)	157.44	123.9	80.66	220.1	144.2	477.9	338.5	137.1	157.1	161.2	85.91	
Biomass g m ⁻²	2.14	0.32	0.01	0.26	0.05	0.70	0.54	0.16	0.01	0.60	0.11	
(± CL)	1.57	0.33	0.01	0.17	0.02	0.41	0.45	.24	0.01	0.50	0.19	
H'	4.09	3.37	2.95	2.52	2.71	3.88	3.24	2.74	2.80	2.25	2.63	
J	0.89	0.94	0.92	0.80	0.92	0.86	0.82	0.90	0.91	0.68	0.83	
Species per 10 individuals	9.0	9.0	8.4	6.8	7.7	8.8	7.8	7.72	8.0	5.7	7.0	
Species per 20 individuals	16.5	16.2	14.2	10.9	12.3	15.6	13.4	12.59	13.5	9.2	12.0	
Species per 30 individuals	23.0	22.5	18.9	14.1	15.5	21.3	18.2	16.32	17.8	12.0	15.0	
Species per 60 individuals	38.6	a	a	20.6	18.1	34.5	29.27	a	a	18.2	a	
Species per 100 individuals	54.4	a	a	a	a	47.2	a	a	a	a	a	
Species per 200 individuals	81.9	a	a	a	a	68.9	a	a	a	a	a	
Species per 300 individuals	a	a	a	a	a	84.9	a	a	a	a	a	

^aSample size was too small to allow calculation of the parameter.

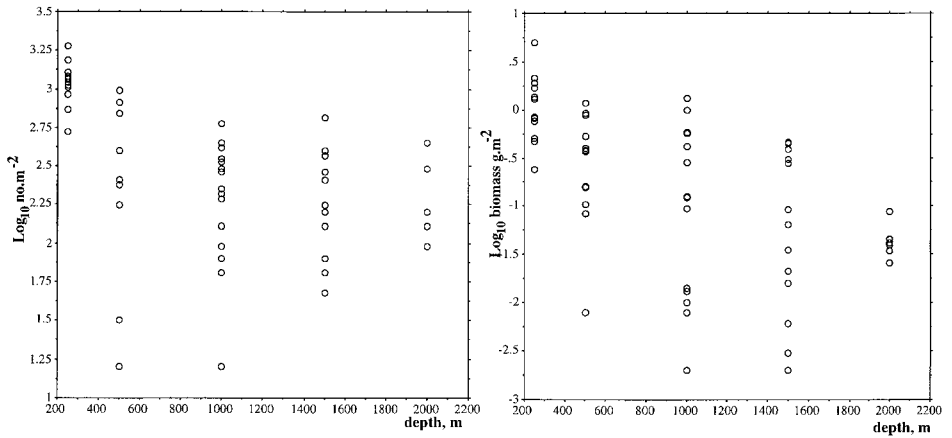


Fig. 3. Density and dry-weight biomass per m^2 vs. depth.

The means of log-density were compared according to the considered depth either as a five-level factor or according to the localization of stations at each depth on flanks or in the channel. For this, the generalized linear models and Tuckey's multiple comparison method (GLIM 4, 1994) were used. Comparison of mean densities at the different depths (homogeneity test $\chi^2 = 69.32$, 4 df, $p < 0.001$) shows that only the stations at 250 m depth have a mean log-density significantly higher than the others ($\chi^2 > 5.6$, 1 df, $p < 0.02$); from 500 to 2000 m depth, the log-densities are apparently not different ($\chi^2 < 3.8$, 1 df, $p > 0.05$). The position of the stations has no apparent effect ($\chi^2 = 8.29$, 10 df, $p = 0.60$).

3.2.3. Biomass

The same method of analysis was carried out on dry weight biomass (biomass m^{-2}). The variation of biomass as a function of depth for individual samples is shown in Fig. 3. The estimated regression equation of the biomass as a function of depth is

$$\text{Log}_{10} (\text{biomass m}^{-2}) = 6.87 - 0.0018X \quad (\text{Fig. 3})$$

(Depth effect, $\chi^2 = 89.62$, 1 df, $p < 0.001$).

Comparison of the mean biomass at different depths (homogeneity test $\chi^2 = 109.0$, df 4, $p < 0.0001$) shows that the difference of the means of log-biomass between any two levels of this factor is significantly different from zero ($\chi^2 > 5.44$, 1 df, $p < 0.02$) except between 1500 and 2000 m ($\chi^2 = 0.53$, 1 df, $p = 0.47$). For stations ($\chi^2 = 156.2$, 10 df, $p < 0.01$), it is only at 500 m depth (CTL 2, CTL7) that no significant difference can be detected ($\chi^2 < 1.54$, 1 df, $p > 0.215$). For the other stations at each depth, log-biomass are different between stations ($\chi^2 > 5.25$, 1 df, $p < 0.022$) depending on their location, whether on channel or flanks, but no systematic relation was apparent.

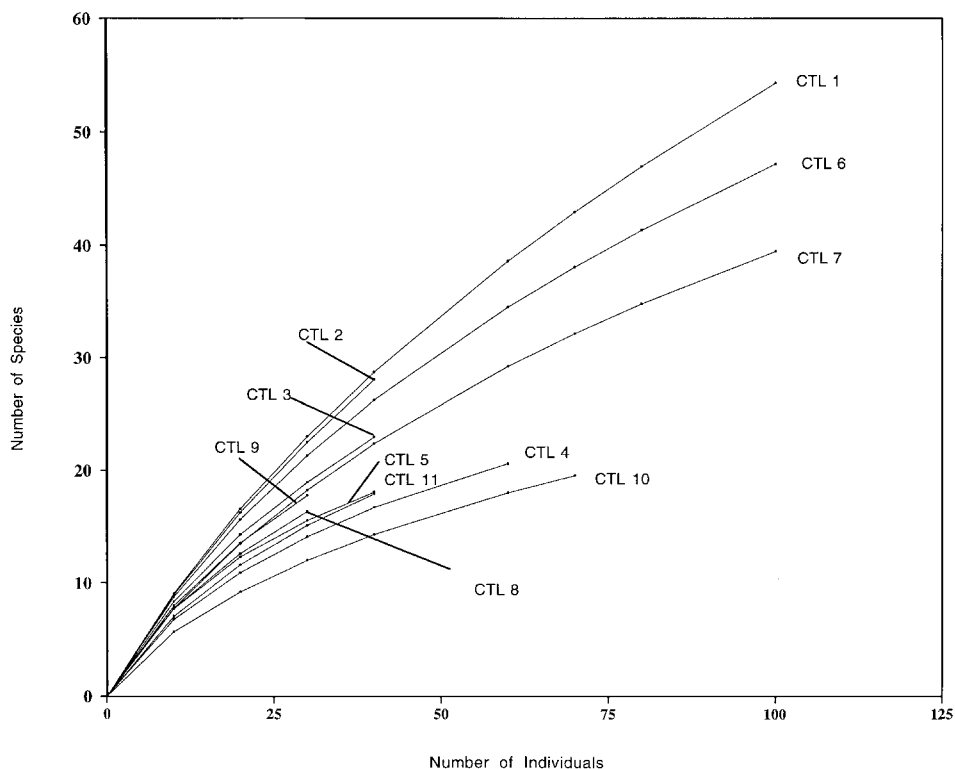


Fig. 4. Hurlbert rarefaction curves for 11 stations sampled at Toulon Canyon. Number of individuals limited to 100.

3.2.4. Diversity

Rarefaction curves (Fig. 4) indicate that the shallower stations are the most diverse in Toulon Canyon. At the same depth, the number of expected species is different in the channel and the flank stations. Nevertheless, the general tendency is a decrease of the diversity according to the depth. Shannon Wiener indexes, ranging from 4.09 bits in the canyon axis at 250 m to 2.71 bits at 2000 m depth, confirm this tendency (Table 3). The evenness is very strong, always greater than 0.80 except for station 10, which gives an evenness of 0.68. There is no particular correlation between the variation of evennesses and increasing depth.

3.2.5. Affinity of the assemblages

Clusters obtained from NESS index ($m = 10$) show that clustering depends on depth and location of stations in the channel and on the flank (Fig. 5). Three groups of stations can be distinguished: (i) stations in the upper part of the channel canyon and the east flank (CTL1, CTL2, CTL6, CTL7); (ii) channel stations from 1500 to 2000 m depth (CTL4, CTL5); (iii) stations located between 1000 and 1500 m depth on the east

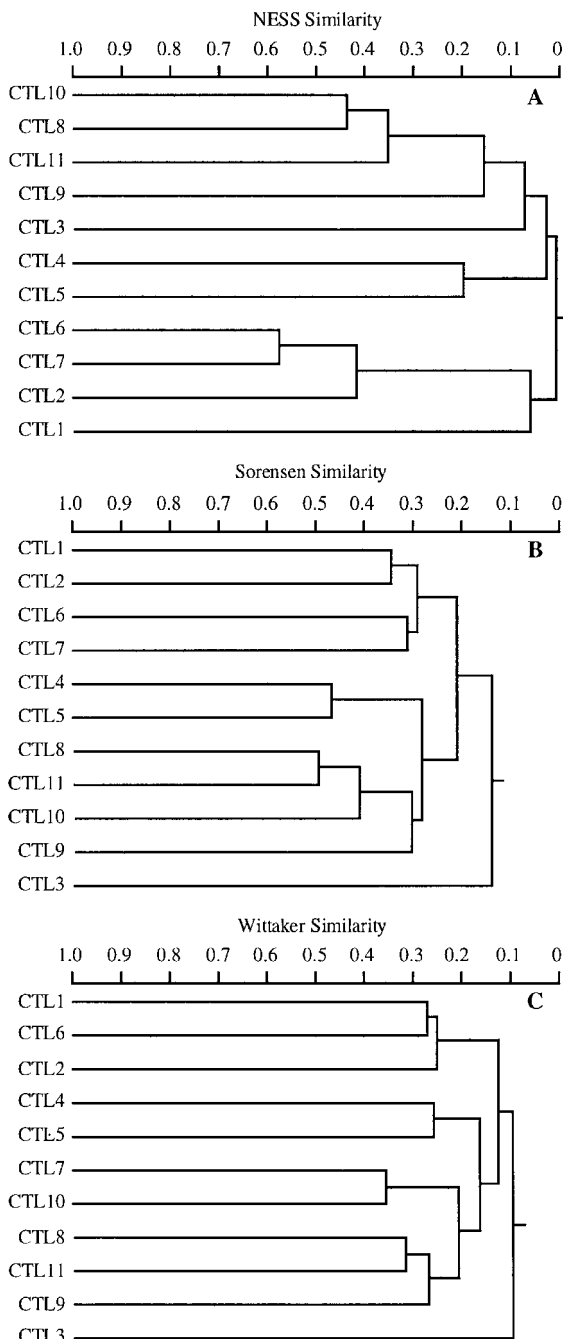


Fig. 5. Dendrogram of Toulon samples clustered with NESS at 10 individuals (A), Sorensen's index (B), Wittaker's index (C) and group average sorting.

and west flanks (CTL3, CTL8, CTL9, CTL10, CTL11). With $m = 30$ (not represented), the clustering remains similar except for the channel station CTL1, CTL2, CTL3 separated from the others stations.

The cluster patterns resulting from Sorensen and Wittaker analysis are similar to those from NESS with $m = 10$, except for station CTL3, completely separated from the other stations for both indexes, and station CTL7, which is grouped with station CTL10 in Wittaker analysis.

For all the similarity indexes, the affinities between stations are far weaker and are always lower than 0.5.

NESS when used at low “ m ” values is dependent on the dominant species (Grasle and Smith, 1976). The weak values obtained with this index and the two others do not result from the presence of rare species at each station but reflect qualitatively and quantitatively the existence of strongly individualized assemblages related to the spatial distribution of the stations.

3.2.6. *Species association*

The clusters obtained from the analysis in R mode are presented in Fig. 6. Taking into account associations of species with affinities most often close to or greater than 50%, nine major groups can be distinguished.

Analysis of the species distribution of each group at the different stations shows that the first group, made up of 17 taxa, associates species that are found most of the time in the whole studied area.

Group 2, subdivided into three sub-groups, is made up of 48 species, most of them colonizing the east flank and the upper slope.

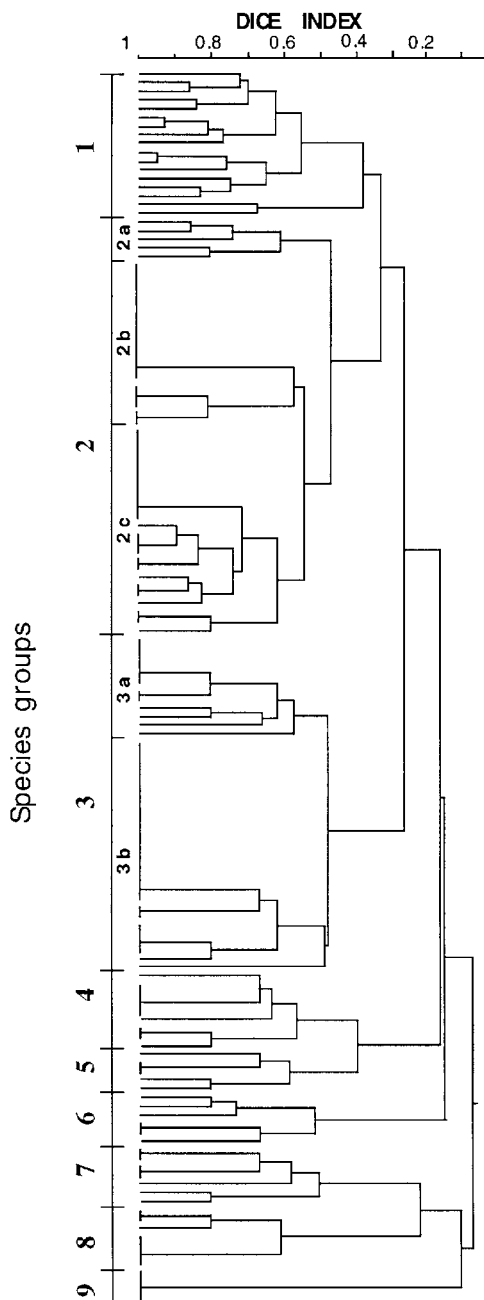
Sub-group 2a (five species) corresponds to species collected on the east flank between 250 and 1500 m depth. Sub-group 2b (19 species) is made up of species colonizing the upper east flank (CTL6), and sub-group 2c (24 species) is made up of species colonizing the upper slope (canyon channel and east flank between 250 and 500 m depth).

Group 3 (39 species) corresponds to species that are limited to the upper part of the canyon channel between 250 and 500 m depth (sub-group 3a, 12 species) and at 250 m depth (sub-group 3b, 27 species).

Groups 4, 5, 6, 7, 8 and 9 are made up, respectively, of the association of 9, 5, 6, 7, 7 and 4 taxa corresponding to species more particularly limited to station CTL 7 at 500 m depth on the east flank for group 4 and group 5, to species limited to deep zones of the canyon channel and west flank for group 6, to species colonizing the west flank stations for group 7 (CTL 11) and group 8 (CTL 10) and to species mainly limited to station CTL 3 for group 9.

It should be pointed out that most of the collected species, except characteristic deep species of the bathyal or abyssal zones (Fig. 6), are eurybathic species commonly occurring in the different assemblages of the Mediterranean continental shelf.

Fig. 7 shows the dominance within the different groups and subgroups, as defined by the analysis in R mode, of eurybathic and deep species. First of all, it can be observed that eurybathic species are dominant in Toulon Canyon compared to deep species. The dominance of these eurybathic species exceeds 75% at all stations except



Group 1

Cyclammina cancellata, *Laonice cirrata*, *Aphelochaeta* cf. *marioni*, *Nuculana tenuis*, *Thyasira flexuosa*, *Aricidea annae*, *Lumbrineris latreilli*, *Lumbrineris gracilis*, *Glycera tessellata*, *Prochatochaeta raduliferum*, ***Onchnesoma steenstrupii***, *Levinsonia gracilis*, *Aricidea monicae*, ***Capitellides giardi***, *Notomastus latericeus*, *Glycera rouxii*, *Nebalia* sp.

Group 2

2a) *Amphilepis norvegica*, *Paradoneis lyra*, ***Aricia kupfferi***, *Glycera* sp., *Nereis hircincola*.

2b) *Amphipholis squamata*, *Amphiuira filiformis*, *Arca lactea*, *Cuspidaria costellata*, *Littorina palliata*, *Modiolus phaseolinus*, *Caulierella bioculata*, *Chloea venusta*, *Onuphis conchylega*, *Phyllococe madeirensis*, *Stylarioides plumosa*, *Ampelisca spinipes*, ***Ebalia nux***, *Haploops dellavallei*, *Aspidosiphon muelleri*, *Ophelia* sp., ***Diastylis cornuta***, *Sthenelais minor*, *Metaphoxus pectinatus*.

2c) *Amphiuira chiaiei*, *Arca pectonculoides*, *Dentalium panormum*, *Chlamys hyalinum*, *Timoclea ovata*, *Amage aspersa*, *Aponuphis bilineata*, ***Aricidea cf. abyssalis***, *Nephthys incisa*, *Syllis cornuta*, *Ascidia conchylega*, *Ampharete grubei*, *Amphicteis gunneri*, *Pista cristata*, *Poecilochaetus serpens*, *Melinna palmata*, *Terebellides stroemi*, *Aricia* sp., *Eunice oerstedii*, *Sabellides octocirrata*, *Onuphis lepta*, *Thyone gadeana*, *Auchenoplax crinita*, *Kellya* cf. *suborbicularis*.

Group 3

3a) *Amphipholis squamata*, *Myrtea spinifera*, *Venus casina*, ***Harmothoe impar***, *Leiocapitella dollfusi*, *Pectinaria auricoma*, *Dilonereis filum*, *Scherocheilus minutus*, *Lucinoma borealis*, *Exogone verugera*, *Golfingia elongata*, *Prinospio steenstrupii*.

3b) *Ophiothrix fragilis*, *Aricidea claudiae*, *Aricidea simonea*, *Capitella capitata*, *Chone filicaudata*, *Cirratulus chrysoderma*, *Dasybranchus caducus*, *Eudalia viridis*, *Euryssyllis tuberculata*, *Harmothoe reticulata*, *Heterocirrus zelandicus*, *Lumbrineris impatiens*, *Paralacydonia paradoxa*, *Platynereis dumerili*, *Cirolana neglecta*, *Inachus dorsetensis*, *Leptocheirus hispidus*, *Lysianassa* sp., *Pagurus prideauxi*, *Clymene gracilis*, *Lumbrineris fragilis*, *Aonides oxycephala*, *Magelona cf. alleni*, *Paradoneis drachi*, *Scalibregma inflatum*, *Arabella iricolor*, *Clymene* sp.

Group 4

Abra longicallus, *Argyrotheca cistellula*, ***Aricidea aberrans***, *Nephthys hystrix*, ***Eriopisa elongata***, ***Calocaris macandreae***, *Marphysa bellii*, *Microdeutopus damnoniensis*, *Pygospio elegans*.

Group 5

Myriochele sp., *Spio multioculata*, *Harpinia crenulata*, *Prionospio cirrifer*, *Paraprionospio pinnata*.

Group 6

Dodecaceria concharum, *Maldane glebifex*, *Scoploptus armiger*, *Nicomache* sp., *Leuconia* sp., *Monticellina* cf. *heterochaeta*.

Group 7

Stylocordyla borealis, *Capitobrancheus* sp., *Chaetozone* cf. *setosa*, *Cirratulus filiformis*, *Magelona* cf. *cincta*, *Palliolium incomparabile*, *Thyasira ferruginea*.

Group 8

Ophiopsila cf. *aranea*, *Prionospio* sp., *Harpinia dellavallei*, ***Brada villosa***, ***Onuphis quadricuspis***, *Stylarioides monilifer*, *Monoculodes* sp.

Group 9

Fauveltopsis brevis, *Levinsonia* sp., *Gammarus subtypicus*, *Idotea baltica*.

Fig. 6. Dendrogram of slope species measured with Dice's index and species making up the different groups. Group 1: species occurring at every depth of the continental slope; Group 2: species mainly restricted to the east flank (2a), the upper east flank (2b) and the upper slope (2c); Group 3: species limited to the upper part of the canyon channel between 250 and 500 m depth (3a) and to 250 m depth (3b); Group 4 and group 5: species mainly limited to station CTL7; Group 6: species mainly limited to the lower slope; Groups 7, 8, 9: species, respectively, limited to station CTL11, CTL10 and CTL3. Species in bold are deep species which are characteristic of bathyal deep mud or abyssal assemblages.

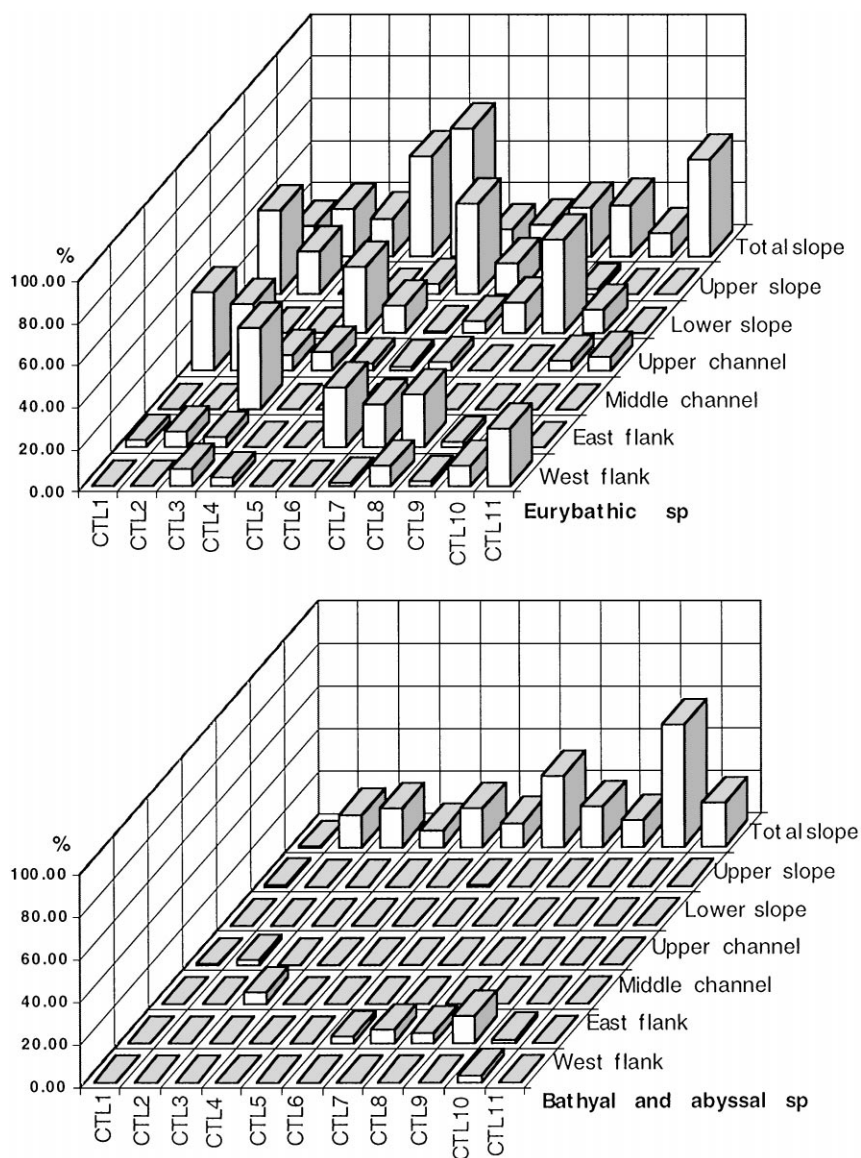


Fig. 7. Dominance at the sample stations of eurybathic and deep species of the different groups defined by analysis in mode *R* (Total slope: group 1. Upper slope: group 2c. Lower slope: group 6. Upper channel: group 3. Middle Channel: group 9. East flank: groups 2a, 2b, 4 and 5. West flank: groups 7 and 8).

for station CTL 7 (60.80%) and station CTL 10 (38.52%), presenting a facies of benthic foraminifera, *Cyclammina cancellata*, that is characteristic of the Mediterranean deep mud assemblage (PICARD, 1965). At the other stations, the dominance of strictly deep species is always less than 25%.

3.2.7. Relation between macrofauna and environmental factors

The factorial correspondence analysis (FCA) was carried out on a contingency table crossing 142 species against 11 stations. The first three axes explain 44.90% of the total data variability (axis 1 = 16.72%, axis 2 = 14.60%, axis 3 = 13.58%). The results are given in Fig. 8, where the plotted projection plane is illustrated by the factorial planes I–II and I–III, of all the stations and species presenting the strongest absolute and relative contributions.

The first axis separates channel stations located between 250 and 500 m depth and the shallowest station on the east slope from all the other stations. These shallower stations are characterized by species that are not related to particular sediment grain size such as *Ophiothrix fragilis* and *Aponuphis bilineata* (wide ecological range species), *Timoclea ovata* and *Syllis cornuta* (mixticolous species living in substrates presenting a mixing of silt, sand and gravel fractions). On the other hand, species associated with the deeper stations on the negative side of the first axis require substrates with strict granulometric compositions such as *Capitellides giardi* and *Onchnesoma steenstrupii* (characteristic species of the muddy bottom bathyal assemblage). One notes a significant negative correlation between the ordination of the variables along axis 1 and the variation in the fraction smaller than 63 μm at the different stations ($r = -0.76$, $p = 0.02$). The variables and species position structuring this axis as well as the obtained correlation demonstrate that the factor responsible for the creation of the main axis is influenced by the increasing gradient of silting from the upper to the lower part of the slope, resulting from hydrodynamic and bathymetric conditions.

Axis 2 contrasts station CTL3 from the other stations. With regard to the species, *Fauveliopsis brevis*, *Levinsenia* sp, which are present only at CTL 3, and *Chaetozone* cf. *setosa*, contribute strongly to the formation of axis 2. As shown in Table 2, CTL1, CTL2 and CTL3, on the positive side of axis 2, are characterized by high levels of organic carbon compared to the other stations. If station 11 is discarded, we observe a positive correlation ($r = 0.63$, $p = 0.03$) between the ordination of the variables and the organic carbon concentrations measured on this axis. The factor responsible for the formation of axis 2, giving rise to the individualization of the upper stations of the axis and their particular enrichment in organic matter, can only be anthropogenic input in the form of the erratic dumping of spoils between stations CTL1 and CTL2.

Except for stations CTL1 and CTL2, axis 3 contrasts the stations above 1000 m depth (CTL6, CTL7, CTL8, CTL3 and CTL10), located on the negative side of the axis, with the deepest stations below 1000 m depth (CTL9, CTL11, CTL4 and CTL5), on the positive side. Among the species responsible for the creation of axis 3, *Laonice cirrata* and *Maldane glebifex*, respectively characteristic and preferential species of the terrigenous mud shelf assemblage, occur and are associated with the deeper stations of the channel. This assemblage normally occurs at outlets of rivers at depths ranging from 30 to 110 m in the Mediterranean Sea (Picard 1965; Salen 1982). The settlement of these species as far down as 2000 m depth is evidence of rapid sedimentation at these depths of fine particles of continental origin (Bourcier et al., 1993). With regard to the sediment composition, the depth of 1000 m is recognized in the Mediterranean

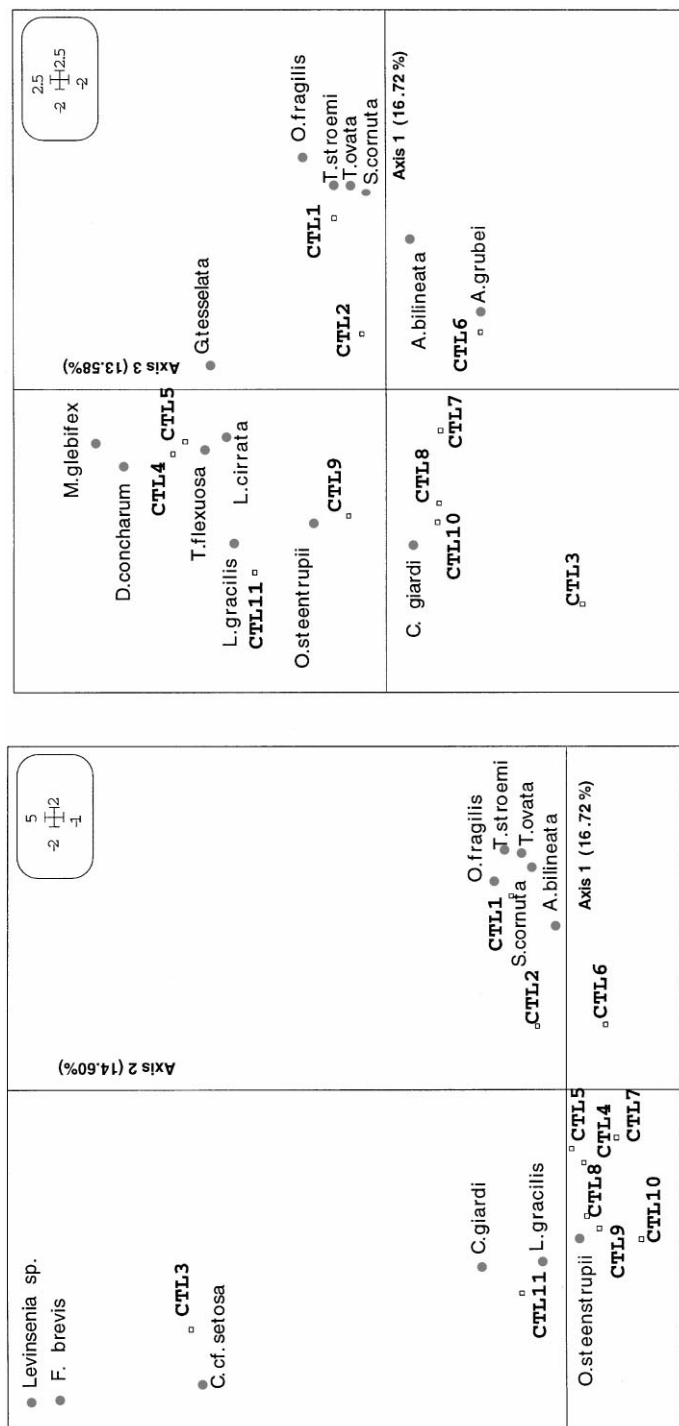


Fig. 8. Results of the correspondence analysis in factorial planes I-II and I-III.

Sea as the boundary separating an upper zone, with dominance of benthic advective contributions transported by the benthic nepheloid layer, and a lower zone, with convective particulate supplies originating from the water column (De Bovee et al., 1990; Buscail, 1991; Bourcier et al., 1993; Poydenot, 1993). The presence of circalittoral biocalcareous sand in the isolated fraction of sieved sediment from Toulon Canyon clearly demonstrates the contribution of the continental shelf over 1000 m depth. Deeper still, one observes mainly pelagic tests such as Pteropoda shells. On the other hand, although not significant at level 0.05, a positive correlation ($r = 0.50$, $p = 0.1$) is apparent between the ordination of variables along the third axis and manganese concentrations measured in the surface sediments. The zones, respectively, influenced by contributions originating from the continental shelf and contributions from the water column presenting high concentrations of heavy metals such as manganese, can be recognized as the third factor responsible for the composition and the structure of the canyon assemblages.

The position of the upper channel stations (CTL1 and CTL2) on the positive side of axis 3 compared to the other upper flank stations could correspond to the channel population's response to the artificial hypersedimentation induced by the dumping of erratic surface dredging spoils at the canyon head.

3.2.8. Distribution of trophic groups

Fig. 9 shows the percentages of the various trophic groups occurring at the studied stations. At most stations, surface deposit feeders predominate and represent between 36 and 73% of the assemblages. The second most strongly represented trophic group is the subsurface deposit feeders, which account for 9–45% of the populations; this is the major feeding mode at stations CTL3 and CTL11. Carnivores (2–30% of the populations) are well represented in the upper stations between 250 and 500 m depth. Suspension feeders have the lowest percentages and represent between 0 and 8% of the assemblages and do not occur in the lower channel.

4. Discussion

4.1. Depth-related patterns

In spite of the relatively homogeneous conditions of temperature and salinity that prevail in the Mediterranean Sea below 300 m depth, patterns of species replacement with depth are similar to these observed in the Atlantic Ocean by Haedrich et al. (1980) and Hecker (1990) for megafaunal and benthic-pelagic fauna or by Rowe et al. (1982) for the macrofauna. However, Gage and Tyler (1991) have noted, on the basis of work by various authors in the Atlantic Ocean, a more gradual replacement of assemblages according to depth for macrofauna than for megafauna. In the Mediterranean Sea, the weak affinity percentages obtained between stations (Fig. 5) are evidence of the sharp change in macrofaunal assemblages according to the depth.

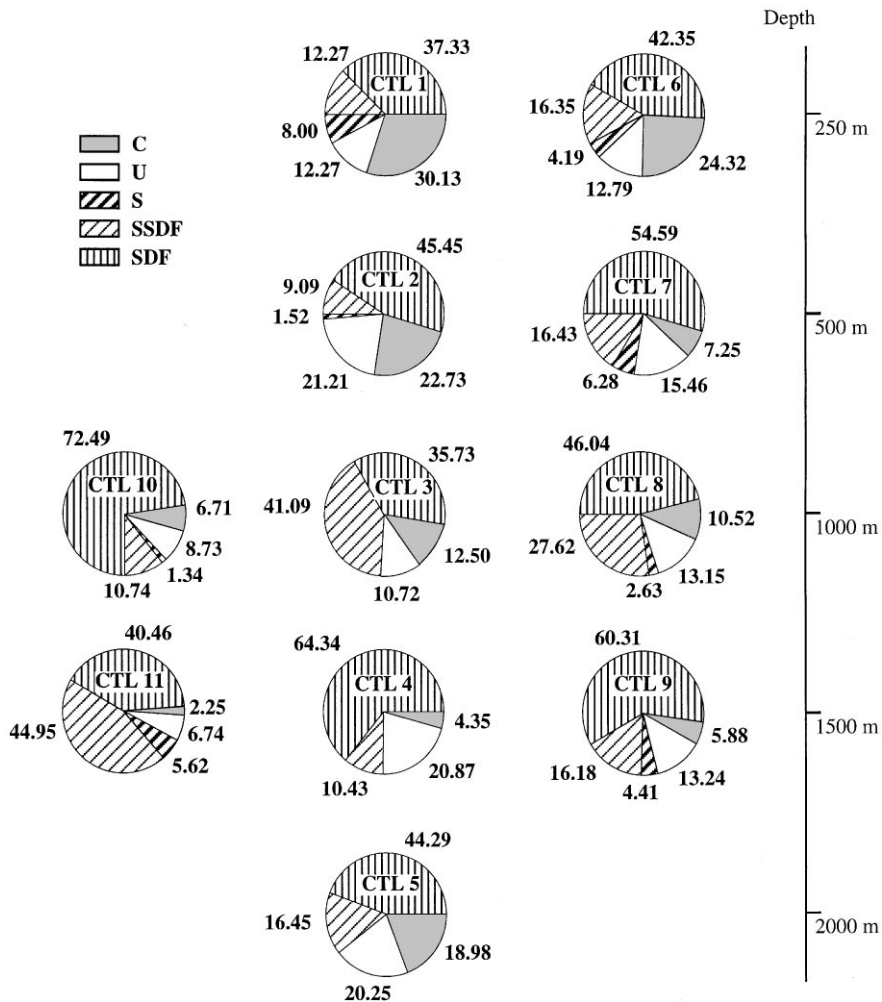


Fig. 9. Percentages of trophic groups at the different stations of Toulon Canyon (C: carnivores; S: suspensivores; SSDF: subsurface deposit feeders; SDF: surface deposit feeders; U: undetermined).

Among the species present in the Mediterranean bathyal zone, Reys (1970) and Carpine (1970) distinguish between eurybathic species with restricted or wide distribution and deep species. Restricted and widely distributed eurybathic species correspond to species found on the continental shelf and slope at depths not exceeding 500 and 2000 m, respectively. Deep species are species strictly limited to the bathyal zone such as characteristic species of the muddy bottom bathyal assemblage or abyssal species that may settle on the continental slope. Most authors who have worked with anchor dredges in the upper part of the Mediterranean slope have stressed the progressive enhancement, with increasing depth, of dominance by characteristic species of the

Table 4
Dominance of characteristic species of deep mud bathyal assemblages at various Mediterranean sites

Sites	Marseille Picard 1965	Monaco Carpine 1970	Canal de Corse Carpine 1970	Rech Lacaze Duthiers Reyss 1970	Toulon present study
Samplers	Anchor dredge	Anchor dredge	Anchor dredge	Anchor dredge	Box corer
Sieve mesh size	1.6 mm	2 mm	2 mm	1 mm	0.5 mm
% deep sp	63.31	60.77	67.36	34.00	16.04

bathyal zone and the decrease of dominance by eurybathic species (Picard, 1965; Carpine, 1970; Fredj and Laubier, 1985; Laubier and Emig, 1993). In Toulon Canyon, eurybathic species predominate from 250 to 2000 m depth, independently of station location (Fig 7).

Table 4 shows the average dominance of deep species present in various bathyal assemblages of the northwestern Mediterranean Sea. Given that the sampling devices, sieve mesh size and sites studied are different, how can we explain the variations in the dominance of these species? With regard to the influence of the site, in spite of the low proportion of deep species observed for the Lacaze Duthiers and Toulon Canyon sites, respectively sampled with anchor dredge and corer, the possibility of a canyon effect, favoring the settlement of eurybathic species to the detriment of deep species, must be rejected. Cores collected in an area that is beyond the influence of the canyon, on the Cassis slope near the Toulon area (Stora et al., 1992), show that dominance of characteristic bathyal species does not exceed 10%. On the other hand, at the different sites studied, regardless of the sampling devices used, the decrease of bathyal species dominance is directly related to the decrease of the sieve mesh size. It would seem that the strong dominance of deep species reported up till now in the Mediterranean bathyal zone is, in fact, more closely linked to the large mesh size of the sieve, which lets small eurybathic specimens pass through that are usually retained on 500 or 250 μ m mesh size (Chardy et al., 1973), than to any real increase of bathyal populations with depth.

The *R* mode analysis shows that Toulon Canyon assemblages are formed in part by a group of ubiquitous eurybathic species occurring in the whole set of stations, associated to individualized species groups that dominate in different parts of the canyon. Since the species forming these groups are also for the most part eurybathic, their settlement pattern does not seem to be linked to optimal life conditions according to the depth (Hecker, 1990), but is rather dependent on the influence exerted in the different parts of the canyon of variable anthropogenic or natural environmental conditions.

4.2. Zonation pattern

“Determining the causes of the pattern of species replacement with depth remains one of the most difficult and elusive problems faced by deep sea ecologists” (Gage and

Tyler, 1991). The surveys by Rex (1981), Peres (1982), Carney et al. (1983), Gage and Tyler (1991), Blake and Grassle (1994) and Blake and Hilbig (1994) show that the main factors that influence species distribution may be of physical origin (temperature, pressure, particle supplies that control grain size distribution, geochemical characteristics and trophic availability of the sediments and currents favoring larval dispersal) or of biological origin (life-history tactics, interspecific competition and predation, trophic strategy).

For the Mediterranean bathyal macrofauna, according to Picard (1965), the main factor governing the distribution of species is the texture of the sediment, while for Carpine (1970) it is the depth and not the nature of the substrate that is significant. REYSS (1970) mentions grain size distribution, depth and the constancy of T/S as the essential factors governing community distribution in the Lacaze Duthiers Canyon. On the other hand, in the eastern Mediterranean sea, food availability is the principal regulating factor according to Tselepidis and Eleftheriou (1992).

The factorial correspondence analysis carried out with Toulon Canyon samples shows in planes I-II and I-III a "V" pattern for variables. This pattern indicates a Gutman effect, which suggests the dominant influence of a common factor responsible for the positioning of the descriptor along axes I, II and III (Benzecri, 1973).

The analysis demonstrates that the common factor governing the distribution and structure of populations is related to the nature and the origin of sediments and more particularly their grain size distribution (fraction smaller than 63 μm : factor 1), geo-chemical composition (factor 2) and mode of transport and sedimentation (benthic nepheloid or originating from the water column) (factor 3). The role of sediment particle size on the composition and the diversity of deep sea macrobenthic communities and the deep species' sensitivity to small differences in grain size has been demonstrated by Etter and Grassle (1992). It is quite evident, however, that the chemical and physical nature of sediments results from the general environmental conditions. The factors identified can have a direct or indirect impact on population distribution. In addition, environmental conditions governing the composition of sediments regulate other factors, notably trophic supply.

Rex (1981) emphasizes that a multiplicity of physical factors must in part underlie patterns of faunal change, but direct evidence on the relative importance of these factors is entirely lacking. This difficulty may be explained by the absence of particular predominant factors, as we can see from the results obtained in the Toulon Canyon. The very close inertia percentages obtained for the three first axes emphasize the absence of hierarchy among the factors influencing the zonation pattern of populations.

4.3. The effect of environmental factors on community structure

4.3.1. Species richness, number of individuals, diversity and evenness

Surveys on this topic (see Rex, 1981; Gage and Tyler, 1991) show that the species richness pattern along a depth gradient follows a parabolic curve. In the Atlantic Ocean, on the continental slope off Cape Hatteras between 500 and 2000 m depth, species richness tends to increase with increasing depth (Blake and Hilbig, 1994).

Table 5
Comparison of infauna assemblage parameters of the Atlantic slope (Hudson Canyon, Rowe et al., 1982) and the Mediterranean slope (Toulon Canyon)

Depth (m)	Hudson Canyon				Toulon Canyon		
	203–570	1141–1437	1707–1815	2351–2673	250–500	1000–1500	2000
Total area of samples (m ²)	0.26	0.11	0.26	0.28	1.5	2.24	0.37
No. of collections	12	5	12	8	24	36	6
No. Species	118	70	105	128	188	60	22
X specimens m ^{−2}	9280	4760	1880	1790	750	246	211
H'	3.35	3.28	3.99	4.28	4.47	3.63	2.71
J	0.7	0.77	0.86	0.88	0.85	0.81	0.92
Biomass g m ^{−2a}	46.2	10.4	9.2	8.2	0.93	0.19	0.05

^aBiomass is respectively wet weight biomass for the Atlantic and dry weight biomass without shell for the Mediterranean Sea.

Table 5 shows the main parameters of macrobenthic communities recorded in and in the neighbourhood of the Hudson canyon by Rowe et al. (1982) and in the Toulon Canyon. While the total number of species between the two sites cannot be compared due to the difference in the surface area sampled, it is nonetheless apparent that in the Mediterranean Sea species richness on the slope decreases regularly according to depth, while it tends to increase in the Hudson canyon.

This decrease in species richness gives rise to a similar decrease in the diversity index according to depth in the Mediterranean Sea, while diversity increases in the Hudson canyon. While the evenness is very similar in Atlantic and Mediterranean Sea from 1500 m depth, in the Mediterranean it is particularly high on the upper slope, demonstrating that most of the species composing the communities occurring between 250 and 2000 m are represented by a very similar number of individuals. It is well known that Mediterranean population density and biomass are particularly low compared to those of the world’s oceans (Peres, 1982). The biomass expressed in dry weight (Table 3) cannot be directly compared at the two sites in the same way as the density; however, the decline of these parameters according to depth observed in Toulon Canyon is consistent with the general tendency widely reported in the literature.

4.3.2. Canyon funneling effects

Canyons induce particular environmental conditions giving rise to the settlement of different macrofaunal and megafaunal populations in the channel and on adjacent slopes (Rowe, 1971; Haedrich et al., 1975, 1980; Rowe et al., 1982; Peres, 1982; Gage and Tyler, 1991; Bourcier et al., 1993). The channel of Toulon Canyon is characterized, especially between 250 and 1000 m depth, by marked sediment enrichment

in organic matter (Table 2). Similar enrichment observed in the upper part of the Hudson Canyon is attributed by Keller et al. (1973) to a shelfward source. In Toulon Canyon, as previously mentioned, the association of strong concentrations in heavy metals and high rates of organic matter shows that the observed enrichment is of anthropogenic origin and is largely the result of dredge spoil dumping at the canyon head.

From the qualitative point of view, the presence of these spoils and deposit channelling constitute both favorable conditions for groups of species exclusively occurring in the channel and, conversely, unfavorable conditions for groups restricted to the flanks. In the canyon axis, the occurrence may be noted of the polychaetes *Capitella capitata*, *Chone filicaudata*, *Platynereis dumerili*, *Leiocapitella dollfusi*, *Pectinaria auricoma*, the crustaceans *Cirolana neglecta*, *Leptocheirus bispinosus*, *Pagurus prideauxi*, the Mollusc *Myrthea spinifera* and the echinodermata *Ophiothrix fragilis* which are eurybathic species proliferating in the Toulon harbours (Bourcier et al., 1979). These species can find in the deposit area conditions similar to those of the Toulon harbours, allowing the larvae settlement. Such observations have been made by Blake and Hilbig (1994) on the continental slope off Cape Hatteras. In this area, the topography and the circulation favor the sedimentation of inner shelf and estuarine sediments on the slope involving a large dominance of shelf species in a bathyal environment. Observations made at Toulon Canyon channel support the Blake and Hilbig (1994) hypotheses about the recolonization of near shore dredge material or other type of sediment dumped onto a continental slope by non slope faunal assemblage.

It is also conceivable at Toulon Canyon that some species, such as molluscs protected by their shells, may have been deposited directly with dredging spoil and be found in survival condition. Moreover, the survival capability of circalittoral species could explain the presence of *Idotea balthica*, sampled at 1000 m at station CTL 3. This species normally proliferates in the littoral zone in plant debris. During planktonic trawls in the canyon area, one of the present authors (J. Le Campion) has collected fragments of *Posidonia* leaves with *Idotea* clinging to them in plankton nets. If dredge spoils and channelled deposits favor the presence of some coastal species in the bathyal zone, in contrast upwellings induced by winds can cause the dispersion and settlement of abyssal species larvae. The polychaete *Fauvelopsis brevis*, collected at 1000 m depth at the canyon axis, has so far never been reported at depths shallower than 2000 m in the Mediterranean Sea (Laubier and Emig, 1993).

From the quantitative point of view, conditions prevailing at the canyon channel, in particular, the sediment enrichment in organic matter, do not entail any particular difference at each depth in comparison with the canyon flanks in the species richness, density and biomass of the resident assemblages. It is of course evident that this does not automatically lead to the conclusion that high rates of organic matter have no influence on these assemblage parameters. Either organic matter is composed of refractory elements that are not usable by the populations (Kripounoff et al., 1985) and therefore has no impact, or the heavy input of organic matter associated with pollutant discharge results in impoverishment of populations in the upper and middle part of the canyon channel (Pearson and Rosenberg, 1978), which in the absence of dredge spoils might have higher densities. Although the differences are not statistically

significant, this last hypothesis is especially supported by the low average densities at station CTL2 of the channel in comparison with the other stations, and conversely by the higher densities at stations CTL4 and CTL5 that are not directly exposed to the effects of the dredge spoils.

4.3.3. *Trophic group distribution*

The distribution of the major trophic groups of bottom invertebrates depends on the availability of their specific food resources, which in turn depends on both the bottom profile and the degree of eutrophy (Peres, 1982). From observations of the epibenthic fauna in the Atlantic Ocean, it appears that generally carnivore/scavengers and suspension feeders predominate on the upper slope, suspension feeders alone predominate in mid-slope and deposit feeders on the lower slope (Gage and Tyler, 1991). At the shelf-slope break, macroinfauna assemblages are dominated by suspension feeders on the shelf side of the shelf break and by deposit feeders on the slope (Blake and Doyle, 1983). In Toulon Canyon, independently of the depth and location of the stations, depositivore species are largely dominant. Below 500 m depth, suspension feeders disappear in the canyon axis, while low percentages of this trophic group remain on the slopes. Similarly, while carnivores are well represented in stations located at 250 m in the canyon channel and on the east flank, a higher percentage of individuals are found in the channel between 500 and 1000 m depth than on the slopes. The trophic structure of the assemblages found in this part of the canyon channel, marked by the disappearance of the filter-feeding species and the maintenance of carnivores, is characteristic of perturbed areas exposed to strong organic inputs (Pearson and Rosenberg, 1978). This trophic structure can only reflect the impact of dredge spoils at the canyon head. On the other hand, the weak dominance of suspension feeders on the upper and median parts of the slope may be related to the low tidal range of the Mediterranean Sea, with the consequent absence of strong, regular currents at the shelf break.

While at most of the stations surface deposit feeders are more numerous than subsurface deposit feeders, the contrary is apparent for the assemblages of stations CTL3 and CTL11, respectively located at 1000 m depth in the canyon channel and at 1500 m depth on the west flank, where subsurface deposit feeders predominate. This pattern of distribution has been described in coastal environments (Rice, 1986; Craig and Lopez, 1994), but has rarely been observed on the continental slope. It would seem that at station CTL3, this predominance of subsurface deposit feeders, mentioned for samples collected at different periods by Gerino et al. (1994), persists. The rapid burying of the organic matter as a result of sedimentary slipping (presence of turbidites) or the biological activity of the megafaunal populations (in particular, burrows of *Calocaris macandreae*) have been suggested as possible explanations of the development of this feeding strategy at station CTL3. It is likely that the same phenomena influence the percentage of subsurface deposit feeders at station CTL11, this below-surface feeding mode being the best strategy for exploiting organic matter resources buried in the sediment column.

5. Conclusions

We are aware that Toulon area, with regard to the Mediterranean Sea as a whole, presents an example of one particular form of continental margin, characterised by a narrow continental shelf and a steep slope. Further studies will have to be undertaken on other types of continental margin presenting different characteristics in order to identify more fully the assemblages of the Mediterranean continental slope. Nevertheless, whether it is a matter here of a specific case or a general pattern, these assemblages present different characteristics from those described in previous studies.

The results show especially that Mediterranean bathyal populations are composed mainly of continental shelf eurybathic species. If characteristic species of the bathyal zone are present, their increasing predominance in the assemblages of the slope as a function of depth has not been confirmed. A marked variability is apparent in the composition of the assemblages according to depth. Analyses have provided some evidence on the factors responsible for the distribution of the populations. With regard to population composition as a function of depth, there is not a single major factor but rather a group of factors acting together, including the sediment grain size, organic matter and pollutant content and mode of sediment transport (benthic nepheloid or by the water column).

The absence of tidal currents influences the trophic structure of the assemblages, which are characterized by a dominance of surface and subsurface deposit feeders compared to suspension feeders and carnivores at the upper and median part of the slope in the Atlantic. Dredge spoil inputs also have an impact on the assemblages of the canyon channel. This impact is marked in the upper part of the canyon. However, it should be pointed out that these inputs do not result in marked degradation of the assemblages as a function of the levels of pollutant and organic matter present, which could indicate a particular resistance or resilience of the bathyal assemblages. Further studies carried out in other perturbed Mediterranean bathyal sites are required to confirm or invalidate this hypothesis.

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